

Changes in social groups across reintroductions and effects on post-release survival

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Abstract

Reintroductions, essential to many conservation programmes, disrupt both abiotic and social environments. Despite growing recognition that social connections in animals might alter survival (e.g. social transmission of foraging skills, or transmission of disease), there has thus far been little focus on the consequences of social disruption during reintroductions. Here we investigate if moving familiar social groups may help a threatened species to adjust to its new environment and increase post-release survival. For a reintroduction of 40 juvenile hihi *Notiomystis cincta* (a threatened New Zealand passerine), we observed social groups before and after translocation to a new site and used social network analysis to study three levels of social change: overall group structure, network associations and individual sociality. We also tested alternate translocation strategies where birds were kept temporarily in aviaries in either a familiar group, or where their prior association was mixed. Although social structure remained similar among juveniles that remained at the source site, we detected significant changes in translocated birds at both the group- and individual- level post-release. However, our holding treatments did not affect these social bonds so we remain unable to maintain or manipulate social groups during translocation. Crucially, there was a small tendency for translocated juveniles that gained more associates during re-assortment of social groups to be more likely to survive their first year post-release. We suggest that prior sociality may not be important during translocations, but rather individuals that are most able to adapt and form associations at a new site are most likely to be the surviving founders of reintroduced populations.

Introduction

Reintroduction, returning species to parts of their range where they have become extinct (IUCN/SSC, 2013), is important for many conservation programmes (Armstrong & Seddon, 2008). A crucial stage that animals must overcome follows their capture, transportation to and release at a new unknown site (collectively 'translocation', IUCN/SSC, 2013), because they must contend with post-release effects and survive to establish a new population (Fischer & Lindenmayer, 2000; Bennett *et al.*, 2012; Parker *et al.*, 2012; IUCN/SSC, 2013; Miskelly & Powlesland, 2013; Armstrong *et al.*, 2017). However, along with changes in the abiotic environment resulting from being abruptly moved to a new site,

such as unknown foraging conditions or altered habitat configuration, reintroductions also change the social environment when the founding group of animals represents a subsample of a larger original population (Ewen *et al.*, 2012b). Key remaining questions in reintroduction biology centre around how animals survive following these multi-level changes created by reintroductions (Anthony & Blumstein, 2000; Armstrong & Seddon, 2008). While the social environment is thought to be important (IUCN/SSC, 2013), there has been less emphasis on understanding the consequences of its disruption.

By leaving behind previous group members or removing external environmental influences on grouping (e.g. food-rich areas that lead to aggregations) (He, Maldonado-Chaparro &

Farine, 2019), moving animals to a new site may result in changes in familiarity (the strength of bonds between individuals) and sociality (an individual's number of associates). Such social changes could affect how well individuals adjust to the post-release environment, and scale up across a released cohort to determine reintroduction success (Anthony & Blumstein, 2000; Armstrong & Seddon, 2008; IUCN/SSC, 2013; Modlmeier *et al.*, 2014; Gil *et al.*, 2018). For example, familiarity can affect post-release dispersal likelihood, as more cohesive groups are less likely to split up (Blumstein, Wey & Tang, 2009; Snijders *et al.*, 2017). Further, continuing to associate with many familiar peers at the release site may allow animals to gather information about their new environment more easily by observing the behaviour of others, which they can then use to offset their own limited experience (Lachlan, Crooks & Laland, 1998; Schwab *et al.*, 2008; Atton & Galef, 2014; but see Ramakers *et al.*, 2016), and adapt quickly to find food or avoid predation (Wong & Candolin, 2014). However, whether animals maintain familiar groups and their social bonds over translocations is not well understood; furthermore, it is unclear if group disruption reduces survival and establishment chances (Armstrong, 1995; Armstrong & Craig, 1995; Jones, Mathews & Porter, 1997; Richard-Hansen, Vié & De Thoisy, 2000; Clarke, Boulton & Clarke, 2003; Shier, 2006).

If familiarity and sociality are important, there might be ways to manage the translocation pathway that allow social groupings to be maintained. Rather than immediately releasing animals, holding groups in temporary captivity (used for disease screening or acclimation to the release site) could develop associations between previously unfamiliar individuals (IUCN/SSC, 2013; Batson, Abbott & Richardson, 2015). Groups integrated in captivity pre-release can be more cohesive and survive better post-release, compared to immediately released groups (Gusset, Slotow & Somers, 2006; Hunter *et al.*, 2007). However, improved group cohesion is not guaranteed (Clarke *et al.*, 2003) and there are other implications of delayed release as it can reduce post-release survival (Castro *et al.*, 1994; Richardson *et al.*, 2013), lower breeding success (Marneweck *et al.*, 2019) or increase stress (Batson *et al.*, 2017). Thus, the benefits of temporary captivity are likely species-specific (Moseby, Hill & Lavery, 2014) and understanding a variety of its advantages and disadvantages (including social cohesion) is important when evaluating its use (IUCN/SSC, 2013).

Social network analysis (SNA) provides a tool to examine detailed changes in group composition and individual social traits, because it can describe differences in associations before and after translocations and we can then test how such changes impact on population stability. This could inform conservation practice by identifying particular social characteristics of groups or individuals that are beneficial to reintroductions. For example, central individuals are crucial for group stability in some social systems, and removing these animals leads to breakdown of group function (Williams & Lusseau, 2006); thus, if such individuals are included in a translocated group it could promote establishment. However, examples applying SNA to studies of

conservation value are rare to date (reviewed by: Wey *et al.*, 2008; Snijders *et al.*, 2017).

Here, we test the effects of reintroduction on group- and individual-level sociality in hihi (stitchbird, *Notiomystis cincta*), an endemic New Zealand passerine. Hihi are a threatened species (Birdlife International, 2017) due to range restriction following habitat loss, and the introduction of non-native predators and competitors. The remnant population was reduced to a single off-shore island (Te Hauturu ō Toi/Little Barrier Island), but since the 1980s, a major aim for their conservation has been reintroduction to predator-controlled areas. Most recent hihi translocations have moved juvenile birds caught at random from the population (Thoroughgood *et al.*, 2013). Juvenile hihi are a social cohort and aggregate throughout late summer and early autumn at the end of each breeding season (Franks *et al.*, 2018), but previous translocations have not taken this sociality into account. Prior to this study it was unknown, therefore, whether translocation altered social groups or what the consequences may be for population establishment. To test if familiarity remains consistent over translocations, (suggesting an intrinsic importance of the identity of associates), we predicted: (1) translocated juvenile hihi would group with individuals they had associated with most strongly (higher familiarity) prior to a translocation. To test if individual-level sociality is also consistent, we predicted: (2) individuals would associate with similar numbers of peers before and after translocation. Alternatively, to test if maintaining captive groups can maintain or promote sociality, we predicted: (3) hihi would group based on who they were held with during temporary captivity. Finally, to show the importance of social changes we predicted: (4) maintaining number of associates would enhance individual survival in translocated hihi.

Materials and methods

Source and release site

In 2017 we reintroduced hihi to Rotokare Scenic Reserve ('release site', 39°27'15"S 174°24'33"E) from Tiritiri Matangi Island ('source site', 36°36'00"S 174°53'21"E; c. 320km from the release site). The source site is a 220 ha island scientific reserve of replanted and remnant native flora which is free of non-native mammalian predators. Hihi were reintroduced to the island in 1995 (Armstrong & Ewen, 2001), and the population (numbering c. 155 total in 2017) is now the main source of birds for ongoing translocations to other sites. The release site (230 ha, including a 17.8 ha lake) is a mainland site of old-growth native forest surrounded by a fence that excludes non-native mammalian predators. Hihi had been locally extinct at the release site and surrounding region for c. 130 years prior to the reintroduction (Angher, 1984).

Defining familiarity before translocation

Between 17 January and 19 March we collected 229 h of observational surveys of 105 juvenile hihi at the source site.

We surveyed all main patches of regenerating native bush on the island (the remainder of the site is characterized by younger flora or more open habitat) and six permanent supplementary feeding stations. Using this method, we monitored known aggregations of juveniles that form every year (three consistent distinct aggregations in 2017, Fig. 1a, see Franks *et al.*, 2018 for more information about group formation), but also captured associations for the few juveniles that did not frequent groups (17/108 juveniles). During each 1-h survey we recorded the identities of juveniles seen within a 15-m radius of the observer (VF): all hihi have an individual combination of coloured leg rings to allow identification by sight. We noted the time of each encounter (to nearest 30 s; if multiple birds were encountered at once we gave them all the same time) and the time each bird left the area (to nearest 30 s) to define associations in our network (see below).

We used package *asnipe* (version 1.1.9) (Farine, 2013) in R (version 3.5.0) (R Core Team, 2018) to build a weighted association network. In the network we considered juveniles to associate if we saw them within 15 min of each other. The 15-min window was determined as a suitable cut-off to describe familiarity based on previous analysis of hihi social groups, where the majority of groups (and individuals) were recorded in an area for a maximum of 15 min (see Supplementary Material). We used this approach to record the network before and after the translocation (see below) to ensure that networks were comparable (Castles *et al.*, 2014), given the practical limitations of incorporating network data collection into the post-release monitoring of the translocated population. The resulting network provided a detailed scaled measure of familiarity between every observed juvenile: a more strongly weighted 'edge' between two juveniles suggested repeated associations across surveys and stronger familiarity; conversely, edge weight '0' suggested a pair of hihi were never observed within 15 min of the other. We detected network 'communities' of frequently co-occurring individuals using the community detection algorithm of Clauset, Newman & Moore (2004) implemented in the *igraph* R package (version 1.0.9, Csárdi & Nepusz, 2006). Each juvenile was assigned a number (1–6) corresponding to its network community. Communities represented the spatially separate groups of juveniles in different gullies at the source site (Fig. 1a). We ensured this community structure was robust prior to analysing translocation effects by comparing our observed network assortment to bootstrapped replicates generated from randomized associations (Shizuka & Farine, 2016), and thus were confident that birds from different communities had limited chances to interact prior to the translocation.

Translocation

Between 27 and 28th March, 40 hihi were caught in mist nets or by capturing birds individually as they entered permanent supplementary feeding stations across the source site (Fig. 1a). We did not control for individual differences in selectivity (likelihood of capture could, for example, depend

on boldness, Madden & Whiteside, 2014), but the same technique has been used across many previous hihi translocations. Therefore, the questions we were asking remained relevant to inform conservation management of hihi. After capture, each bird was disease screened (Ewen *et al.*, 2012a) and then released into one of three pre-existing aviaries (one large enclosure divided into three flights, each measuring $c. 5 \times 3 \times 2.5$ metres) which have been used in many translocations. The aviaries were separated by double-walled shade cloth and filled with dense natural vegetation so that visual contact between aviaries was extremely limited, if not impossible, but hihi were not in auditory isolation from each other or free-living birds. Each aviary held balanced numbers of birds. Each juvenile was assigned to an aviary based on its community in the network before translocation (Fig. 1b): one aviary contained birds from one community ('familiar' group), while the remaining two aviaries contained birds from any community ('mixed' groups, the management used in previous translocations).

All birds for translocation were caught within 24 h, then kept in the aviaries for four further days while disease screening was completed. During holding we provided supplementary food twice daily (Ewen *et al.*, 2018). On the evening of 1 April, hihi were re-caught from the aviaries, health-checked and transferred to translocation boxes (each box contained five hihi caught randomly within an aviary, and we maintained aviary groups of familiar and unfamiliar birds in separate boxes). We transported all birds in one night from the source site to the release site, and all hihi were released successfully the following morning (2 April) at two locations in the release site $c. 200$ m apart. Familiar birds were all released at one location, one aviary of unfamiliar birds was released at the second location, while the remaining unfamiliar aviary was split between the two sites so there was an equal number of birds released at each site [we accounted for aviary number in analyses to include potential differences (see below), but none were found].

Defining familiarity after translocation

We recorded associations at both the release site and source site from 3 April to –3 June 2017 in a similar manner as before translocation. Re-recording associations at the source site while also observing hihi at the release site helped us to understand the drivers of social changes in translocated hihi, because it provided us with a group that had experienced network disruption but were not translocated. For example, if non-translocated birds maintained associations but translocated birds did not, this would suggest that the translocation caused disruption. Hihi were expected to move around the release site during the post-release phase, so we walked pre-established survey lines at both sites to locate juveniles and record comparable data (covering all forested areas at both sites at a maximum of 150 m separation; maximum detection distance for hihi is 80 m, Richardson & Ewen, 2016). Whenever we encountered any juveniles, we noted each bird's colour ring combination, the time it was encountered to the nearest minute and the time it left an area of 15 m

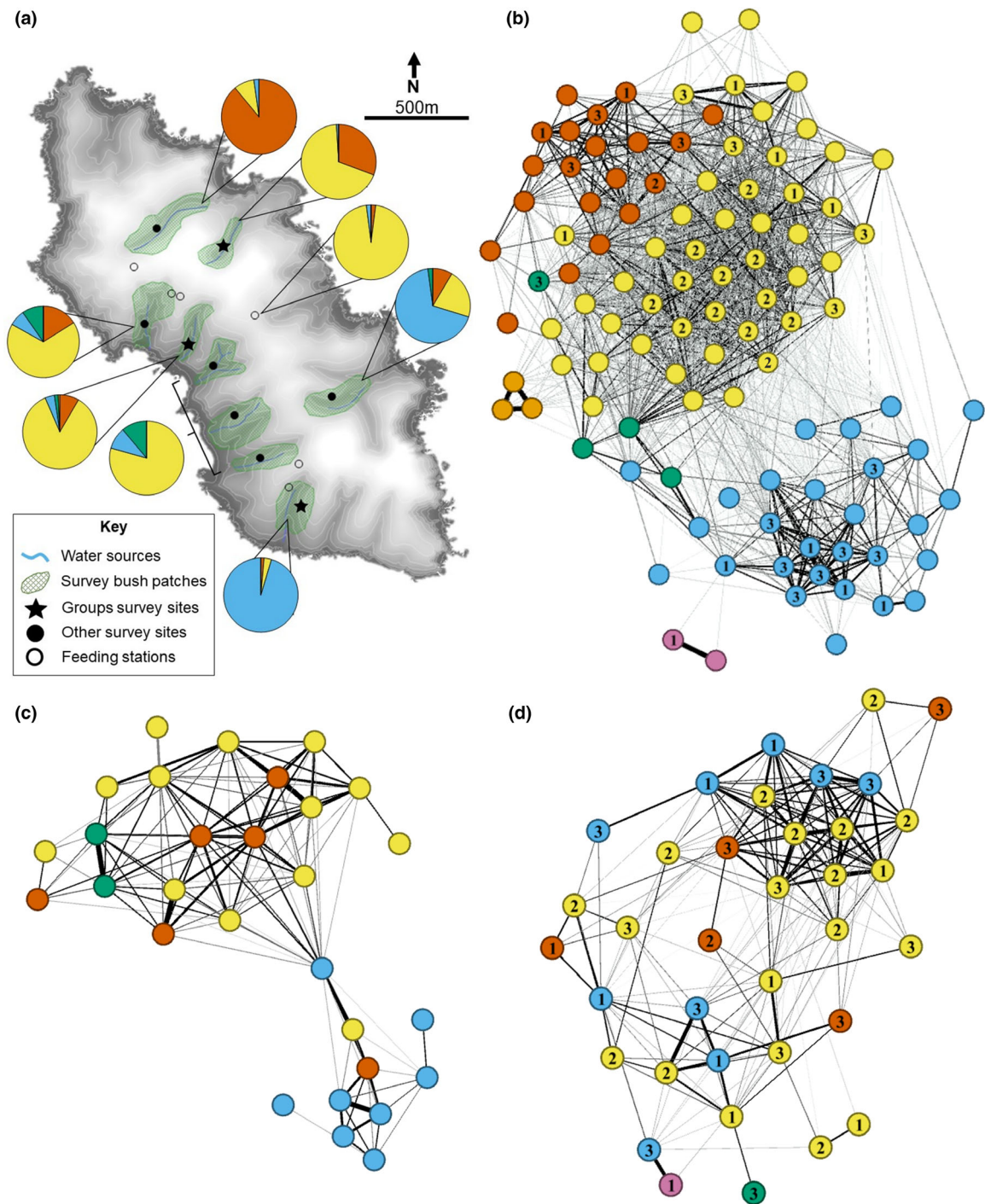


Figure 1 (a) Survey locations used to determine familiarity pre-translocation in main bush patches at the source site (green areas; rest of source site is younger regenerating native flora), including both gully sites (filled circles) and feeding stations (open circles). Pie charts represent spatial distribution of each network community from (b) across the different bush patches (as proportion of number of days each bird from each community seen in each bush patch). Some bush patches are grouped to represent comparable numbers of hihi. Base map contains data sourced from the *LINZ Data Service* licensed for reuse under CC BY 4.0; (b) hihi social network before translocation; (c) network recorded after translocation at the source site; and (d) network recorded after translocation at the release site. For (b–d) nodes (coloured circles) represent each hihi and the edges (lines) represents co-occurrence in a group. Edge width is proportional to number of co-occurrences. Nodes are coloured by network community before translocation (1–6); for full colour version please see online issue. Numbers in (b) and (d) correspond to translocation aviaries. Network arrangement minimizes edge lengths and clusters together frequently associating nodes.

radius too quickly for us to follow (observations by MM and CA at the release site: 300 h, 38 individuals, with two translocated juveniles never seen post-release; by VF at the source site: 100 h, 40 individuals; all observers had similar experience of surveying hihi as part of the standard monitoring of the source population). Finally, we constructed networks for source and release sites separately, using the same method as before translocation based on dividing observations into time windows of 15 min. We accounted for number of observations (both before and after translocation) in our later analyses, in case observing individuals different amounts impacted on social network measures.

Post-release survival surveys were conducted by MM at the release site every month between May and September 2017, and in March 2018. Each survey was constant effort (40 h over 5 days), and involved walking survey lines that covered the entire release site (the same area where we recorded post-release associations). We recorded whether each translocated hihi was sighted (yes = 1, no = 0). We also used similar surveys at the source site in April, May, September 2017 and February 2018 to record sighting/non-sighting of non-translocated individuals. We used these data to investigate links between changes in social networks and monthly survival for translocated birds, which we might expect if losing social connections was disruptive or stressful for hihi, and to compare their survival to non-translocated hihi.

Data analysis

Did translocation change group associations?

SNA was conducted in R. First, we explored if hihi that formed groups before translocation were also more likely to group after translocation. We considered how strong network associations were between hihi depending on their (1) social network community before translocation (community from entire network before translocation = 1–6); and (2) aviary during the translocation ['1' (mixed); '2' (familiar); '3' (mixed)]. For each analysis, we calculated an assortativity coefficient (r , a value from +1 for total association between individuals with the same characteristics, to -1 for total disassociation) using the R package assortnet (version 0.12) (Farine, 2014). Thus, if before-translocation groupings remained, we expected strong positive assortment by pre-translocation network community; alternatively, if maintaining groups in aviaries was important, we expected the strongest positive assortment between birds from the familiar aviary in comparison to unfamiliar aviaries. Networks are non-independent and violate the assumptions of many statistical tests, so we calculated whether assortment was significant by comparing the r value of our network to the r values of 1000 networks generated using pre-network data permutations (P -values specified as P_{rand}) (Farine & Whitehead, 2015; Farine, 2017). Finally, to give a comparison of whether groups changed even if birds were not translocated, we repeated analyses of assortment by pre-translocation community using the source site network after translocation.

Next, we investigated if association strengths between each pair of translocated hihi were similar before and after translocation. We constructed a smaller before-translocation network that contained only the 38 translocated hihi (2/40 translocated birds were never seen post-translocation). We used a Multiple Regression Quadratic Assignment Procedure with Double Dekker Semi-partialling (Dekker, Krackhardt & Snijders, 2007) to investigate the likelihood that the strength of association before translocation predicted that a similar association occurred between the same birds following translocation (VanderWaal *et al.*, 2014; Farine & Whitehead, 2015). We also included a further covariate of aviary number ['1' (mixed); '2' (familiar); '3' (mixed)] to assess whether grouping previously familiar birds during temporary captivity affected associations. Again, we compared this to 1000 permuted networks to determine significance of any effects. Finally, we repeated this analysis using a network of the 40 non-translocated juveniles, to compare how associations changed for birds that remained in the original environment.

Did individuals remain consistent in their sociality?

We investigated if individual sociality remained consistent following translocation, relative to other individuals. For every juvenile, we calculated a weighted degree centrality (degree) before and after translocation, which explained both each bird's number of associates and the strength of its associations. To calculate degree before translocation, we used the network containing all observed juveniles to quantify each bird's maximum possible associations. After translocation, degree was calculated within the respective networks from the source and release sites. As population sizes were different before and after translocation (meaning that different numbers of associates were possible, which could bias degree scores), we ranked individuals by their degree within each network and divided ranks by the size of each population so all were bound between 0 and 1. Therefore, more social birds within each network ranked closer to 1. If individual sociality was consistent, we would expect an individual's rank to remain the same relative to others within their population: for example, a bird of middle-ranked sociality (0.5) before translocation would also have middle-ranked sociality following translocation relative to all other birds at the release site. We assessed what predicted degree rank after translocation using a beta-regression model implemented from the R package betareg (version 3.1-2) (Cribari-Neto & Zeileis, 2015), where our predictors included degree rank before translocation, population (translocated or not translocated) and sex (translocations could affect male and female hihi differently, Armstrong *et al.*, 2002, 2017). We included an interaction between degree rank before translocation and population type, because sociality could change more extensively if moved to a new site. Finally, we included number of observations after translocation as a fixed effect to ensure variation in degree rank was not due to differences in detection.

To assess whether maintaining familiar groups during translocation limited disruption of individual sociality, we calculated each translocated juvenile's change in degree rank from before to after translocation (between -1 and 1 ; a negative value represented a decrease in social rank while a positive value was rank gain). We used a Linear Model with rank change as the response. Our predictors included the aviary type each bird was housed in as 'familiar' or 'mixed'; initial exploratory analysis (not presented) showed no variation in rank change between the two mixed aviaries, so we only compared changes between the different social management types. Degree rank before translocation was included in interaction with aviary type (changes due to aviary management could depend on how social birds were), and we also included sex. Finally, for this analysis we included number of observations both before and after translocation as predictors, because change in rank score could be dependent on variation in both numbers of observations. Again, we assessed significance of all degree rank analyses using data-stream permutations.

Did social changes during the translocation affect survival?

For translocated birds, using presence/absence in monthly surveys we estimated survival depending on change in degree rank (-1 to $+1$: covariate) with a live-recaptures (Cormack-Jolly Seber) analysis in Program MARK (version 9.0) (White & Burnham, 1999). Our global model analysing survival was *sex* \times *degree rank change* + *month* \times *degree rank change* which considered if monthly survival was affected by the extent of change sociality after translocation, explaining both loss and gain of associates relative to all other translocated juveniles. We considered rank change in interaction with sex because disruption could have affected male and female survival differently (Panfylova *et al.*, 2016), and time point because effects of social changes may have changed as birds became more established. We did not analyse survival depending on aviary management, following evidence that there was no significant difference in degree rank change between aviary types (see Results). We compared a set of models with all combinations of predictors by ranking them by their corrected quasi-likelihood Akaike information criterion values (QAICc, due to adjusting for a small level of overdispersion using median $\hat{c} = 1.30$ following initial goodness-of-fit testing). For models with $\Delta\text{QAICc} < 2$, we used model averaging to calculate effect sizes and 95% confidence intervals depending on model weight (which explained relative likelihood of each model). Any parameter with a confidence interval that did not span zero was considered to have a significant effect.

We analysed survival in non-translocated birds depending on degree rank change and sex in the same manner, to provide a comparison from birds remaining at the source site (correcting for median \hat{c} value of 1.42). We could not combine both translocated and non-translocated birds in one survival analysis to explore interactions with site statistically, as the time points of the surveys differed.

Results

Did translocation change group associations?

Juveniles that were not translocated continued to group with individuals from the same communities as before translocation ($r = 0.14$, $P_{\text{rand}} = 0.01$, Table 1; Fig. 1). However, translocated juveniles behaved differently: they were not significantly more likely to form groups with birds from the same pre-translocation community than unfamiliar birds ($r = -0.01$, $P_{\text{rand}} = 0.19$, Table 2a; Fig. 1). Nevertheless, for both translocated and non-translocated hihi, the specific identities of who they associated with changed: association strengths between pairs of juvenile hihi at the source site were not the same before and after the translocation, and birds that associated before translocation were not significantly more likely to associate at the release site (Table 3). Managing social groups in translocation aviaries did not promote group formation post-release, even when birds had been familiar at the source site: in fact, there was a tendency

Table 1. Mixing matrices of association weights for hihi at the source site after the translocation based on network community before translocation (colours correspond to Fig. 1b)

Community	Red	Yellow	Blue	Green	a_i^w
Red	0.07	–	–	–	0.29
Yellow	0.15	0.19	–	–	0.42
Blue	0.04	0.03	0.11	–	0.19
Green	0.03	0.04	0.00	0.03	0.10
b_i^w	0.29	0.42	0.19	0.10	1.00

a_i^w are the row sums, b_i^w are the column sums; due to rounding, sum values may not be exact. Tables are symmetrical, so only half of the values are shown.

Table 2. Mixing matrices showing association weights for hihi at the release site after translocation based on (a) network community before translocation (colours correspond to Figure 1b); and (b) aviary number and category during translocation

(a)	Red	Yellow	Blue	Green	Purple	a_i^w
Red	0.01	–	–	–	–	0.08
Yellow	0.05	0.35	–	–	–	0.59
Blue	0.02	0.19	0.10	–	–	0.32
Green	0.00	0.00	0.00	0.00	–	0.00
Purple	0.00	0.00	0.01	0.00	0.00	0.00
b_i^w	0.08	0.59	0.32	0.00	0.00	1.00

(b)	1 (mixed)	2 (familiar)	3 (mixed)	a_i^w
1 (mixed)	0.06	–	–	0.28
2 (familiar)	0.11	0.12	–	0.38
3 (mixed)	0.11	0.14	0.09	0.35
b_i^w	0.28	0.38	0.35	1.00

a_i^w are the row sums, b_i^w are the column sums; due to rounding, sum values may not be exact. Tables are symmetrical, hence only half of the values are shown.

Table 3. Effects of association strength before translocation on the probability the same two hihi also associated following translocation, for translocated and non-translocated hihi

Group	Covariate	Coefficient	P_{rand}
Non-translocated hihi	Intercept	0.045	0.80
	Association strength before translocation	0.066	0.43
Translocated hihi	Intercept	0.026	0.99
	Association strength before translocation	0.050	0.31
	Aviary (1–3)	0.002	0.51

For translocated hihi, we also considered the effect of holding familiar birds together during temporary captivity on likelihood of maintaining associations following translocation, in comparison to two aviaries of mixed familiarity. Significance of effect sizes calculated using a MRQAP permutation approach.

for weak disassociation in groups of translocated birds kept in the same aviary (Table 2b; $r = -0.09$, $P_{\text{rand}} = 0.04$, Fig. 1) and translocated hihi that shared an aviary did not form stronger bonds with each other than unfamiliar individuals (Table 3).

Did individuals remain consistent in their sociality?

Juvenile hihi that were more social before translocation did not maintain a similar social rank after the translocation, regardless of whether they remained at the source site or were moved to the release site (both pre-translocation degree rank, site and their interaction were non-significant in predicting post-translocation sociality: Table 4a; Fig. 2a). Post-

translocation social ranks did not differ between males and females (Table 4a) and also did not vary depending on how many times a bird was re-sighted any more than expected by random chance (Table 4a). When comparing among translocated hihi only, some birds experienced greater degree rank changes than others (greatest rank gain = +0.59; greatest rank loss = -0.68). However, the amount of change was not predicted by their degree rank before translocation so both more- and less-social individuals were equally likely to change rank (Table 4b; Fig. 2b). Individual degree rank was also not preserved by holding a juvenile with familiar group-mates in an aviary, as there was no significant difference in degree rank change between birds housed in familiar and mixed aviaries (Table 4b; Fig. 2b; this effect was non-significant even while familiar birds were actually more social than mixed-aviary birds as they had come from our largest network community). Finally, the extent of rank change was not significantly different between males and females (Table 4b), and was not significantly affected by re-sighting before or after translocation (Table 4b). Together this suggests that individuals were not consistent in their degree of sociality, and that this did not depend on whether they were translocated, or stayed behind at the release site.

Did social changes across the translocation affect survival?

Although we could not predict rank change, among translocated hihi there was a tendency for birds that experienced a greater decline in degree rank to have poorer post-release survival: the best-supported model explaining monthly survival included rank change and sex as covariates, while accounting for varying re-sighting between sexes (Supporting Information Table S1a). However, monthly survival was high

Table 4. Results of (a) beta-regression model analysing variation in post-translocation degree ranks and (b) Linear Model analysing change in relative degree ranks for translocated hihi

		Coeff.	SE	z	P-value	P_{rand}
(a)						
Degree rank after translocation ~	Intercept	-1.99	0.47	-4.29	<0.001	0.16
	Degree rank before translocation	0.97	0.63	1.55	0.12	0.21
	Site (source site)	1.70	0.54	3.14	0.002	0.25
	Sex (male)	0.22	0.22	0.99	0.32	0.22
	Number of sightings after translocation	0.14	0.02	5.65	<0.001	0.45
	Before translocation degree rank \times site (source site)	-1.30	0.81	-1.61	0.11	0.27
(b)						
Change in degree rank (translocated hihi) ~	Intercept	-0.05	0.64	-0.07	0.95	0.95
	Degree rank before translocation	-0.84	0.80	-1.05	0.30	0.75
	Aviary category (mixed)	-0.04	0.66	-0.06	0.96	0.69
	Sex (male)	-0.05	0.06	-0.90	0.37	0.22
	Number of sightings after translocation	0.34	0.01	8.26	<0.001	0.23
	Number of sightings before translocation	0.01	0.01	0.88	0.39	0.16
	Degree rank before translocation \times aviary category (mixed)	0.20	0.72	0.27	0.79	0.51

P-values generated from the original model are presented, but only for comparison to the P-values generated in relation to coefficients from 1000 randomized networks (P_{rand}). Significant P-values are indicated in bold font.

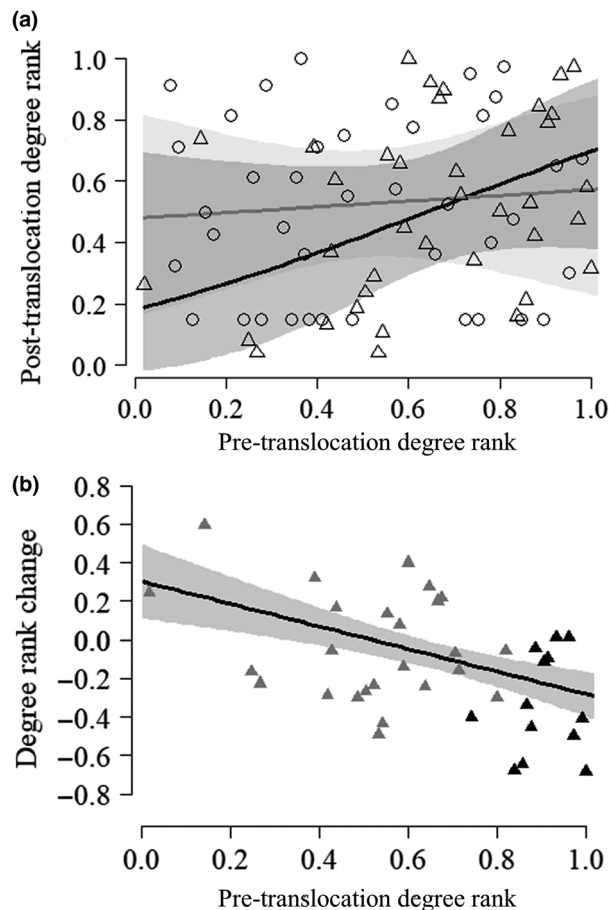


Figure 2 (a) Relationship between degree ranks before and after translocation for non-translocated (circles, grey line) and translocated hihi (triangles, black line); (b) change in degree rank after compared to before translocation for translocated hihi held in mixed aviaries (grey triangles) and the familiar aviary (black triangles). Grey polygons represent 95% confidence intervals from models in Table 4.

Table 5. Model estimates of monthly post-release survival and re-sighting for translocated male and female juvenile hihi

	Survival ϕ		Re-sighting ρ	
	Effect \pm SE	95% CI	Effect \pm SE	95% CI
Male	0.91 \pm 0.03	0.80–0.96	0.94 \pm 0.04	0.82–0.98
Female	0.88 \pm 0.05	0.73–0.96	0.84 \pm 0.07	0.67–0.93

Calculated from model averaging top-ranked models in Supporting Information Table S1a.

overall (Table 5) so the effects of degree change and sex were weak: models with no variation in survival were included in the set with $\Delta\text{QAICc} < 2$ (Supporting Information Table S1a). Survival rates were not time-dependent (Supporting Information Table S1a), so we estimated overall 11-month survival likelihood based on the model averaged monthly survival estimates. Although 11-month survival

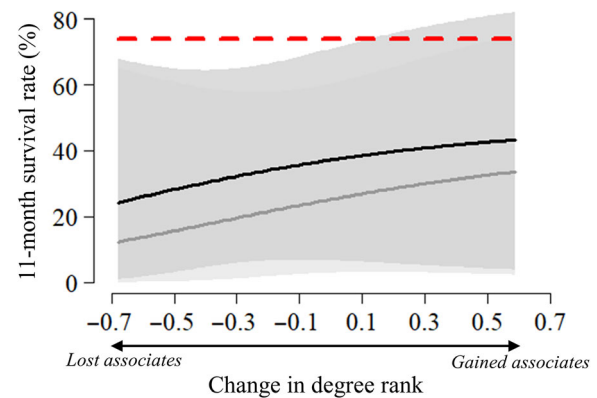


Figure 3 Predicted 11-month post-release survival likelihood depending on change in degree rank after translocation at the release site, for males (black line) and females (grey line). Grey polygons represent 95% confidence intervals. Red dashed line represents survival estimate from non-translocated birds over the same length of time and shows no variation with degree rank change. All predictions extrapolated from monthly survival estimates from top-ranked Cormack-Jolly Seber monthly survival models in Supporting Information Table S1.

predictions were more uncertain, survival varied from 17.4% (95% CI = 0.2–66.7) with the greatest loss of rank (−0.68), to 38.2% (95% CI = 3.0–78.4) for the greatest rank gain (+0.59) (Fig. 3). Overall male survival was 38.1% (95% CI = 12.7–64.6) and female survival was 24.5% (95% CI = 3.3–57.5) (Fig. 3). For comparison, there was little evidence that degree rank change explained survival for non-translocated juveniles (Supporting Information Table S1b) and little support for variation with any other predictor (many models were similarly ranked by ΔQAICc ; Supporting Information Table S1b).

Discussion

Studies contrasting the effects of different treatments on conservation outcomes provide essential evidence to apply reintroduction biology effectively (Taylor *et al.*, 2017). Reflecting this statement, we have provided a detailed investigation of the outcomes of managing group structure and individual sociality during a reintroduction of 40 juvenile hihi, and assessed consequences for survival (Snijders *et al.*, 2017). We have shown that translocating juvenile birds affected their overall social structure, and at a new site they did not remain in the groups they had formed prior to translocation. This was in contrast to hihi that remained at the source site, where group structure was similar after the translocation (although an individual's closest associates were not consistent). Holding juveniles together in an aviary did not maintain or promote group cohesion; instead, there was a suggestion that translocated birds actually disassociated from aviary-mates post-release. At the individual level, there was no evidence that any hihi maintained a similar level of sociality following translocation. Even though we

could not predict sociality loss, translocated juveniles that gained the most associates relative to their previous sociality showed a tendency to survive better (equivalent of maximum 20% higher survival in the first year post-release), although this finding requires more data to be confident that it is significantly different to a null model. Our results therefore suggest that translocation created a disruption to the social environment at both the group and individual level, and this may have consequences for likelihood of establishment that warrant future consideration.

Group-level structure changed for translocated hihi only, resulting in mixing of previously less-associated birds following translocation. However, while group structure only changed for translocated individuals, specific associations and individual sociality did not remain consistent for either the translocated or source site populations, similar to findings in other New Zealand bird species (Armstrong, 1995; Armstrong & Craig, 1995). Together, this suggests that the process of translocation removed key external influences from the source environment that previously maintained hihi groups, and initiated extensive behavioural disruption. Ultimately, if environmental factors at the source site influence group structure, the specific identities of previous associates may be less crucial to group structure over effects from the new site (Moseby *et al.*, 2018). Furthermore, it may mean that groups will never be maintained during reintroductions, which by definition involves removing animals from one environment and placing them at a new site (Ewen *et al.*, 2012b; IUCN/SSC, 2013). An important caveat to our study was that we considered whether associations were maintained over the full post-release monitoring period, including immediately post-release when birds were most disrupted and unfamiliar with the release site. However, it is possible that the strength of changes in social associations could vary during initial dispersal and later settlement, reflecting other progressive changes in behaviour post-release (e.g. Metcalf *et al.*, 2019). Unfortunately, the size of our dataset meant that our statistical power was too limited to split observations and consider how sociality changed over the settlement period. Furthermore, there is also evidence that this settlement gradient can be very variable and difficult to predict (post-release effects have been detected from 1 month to 1 year across previous translocations of hihi, Armstrong *et al.*, 2017). Increasingly, automated data collection methods are becoming available that may allow for more in-depth analysis of potential temporal shifts in associations in the future (Farine, 2018), including for hihi where we are currently developing such monitoring tools.

Even when the identity of associates is not crucial, there may still be consequences for individual survival if both physical and social environments change abruptly. In such cases, social conditions following disruption may be particularly important (Jones *et al.*, 1997): for example, feral horse *Equus caballus* foals that gained associates following an abrupt change (removal of 40% of the population) were more likely to survive (Nuñez, Adelman & Rubenstein, 2015). Although statistical support was weak, our data showed the same trend whereby hihi that became the most social showed a tendency

to be most likely to survive in the translocated population. Conversely, there were no such survival impacts for non-translocated hihi. Gaining associates in an unknown environment may be beneficial by facilitating crucial behaviours that impact on survival, such as efficient co-feeding (Maldonado-Chaparro *et al.*, 2018); alternatively, individuals that survive longest may also have more opportunity to gain associates. Whether this beneficial relationship becomes clearer with more power (i.e. a larger sample size) warrants further investigation, particularly considering that post-release survival was high for this reintroduction (by comparison, previously Panfylova *et al.* (2016) reported just 19% female survival 6 months post-release). Social effects could then be incorporated with evidence for other individual-level effects on survival (Goldenberg *et al.*, 2019), such as exploratory tendency or boldness (Brenner-Harrison, Prodohl & Elwood, 2004; May, Page & Fleming, 2016; Germano *et al.*, 2017; Richardson *et al.*, 2019), or physiological condition (Adams *et al.*, 2010; Cabezas, Calvete & Moreno, 2011) to help inform conservation strategies and select individuals with the best suite of characteristics that might predict a successful translocation (see Parlato & Armstrong, 2013).

Holding animals together in temporary captivity pre-release is thought to promote group cohesion and improve the survival of translocated individuals (Gusset *et al.*, 2006; Shier, 2006; Shier & Swaisgood, 2012; IUCN/SSC, 2013). However, as survival can actually decrease following delayed release in some species, multiple benefits and costs of such a strategy (including practical considerations such as time needed to catch animals) may need to be weighed on a species-by-species basis (Richardson *et al.*, 2013; Moseby *et al.*, 2014; Batson *et al.*, 2015). In hihi, associations were not significantly maintained if birds were housed in a familiar group compared to a mixed group, and neither was individual sociality (degree rank). In fact, groups kept in aviaries together actually indicated a tendency to avoid one another following release. Therefore, there does not appear to be a benefit of temporary captivity for maintaining or establishing a social environment during hihi translocations. This complements previous research investigating other costs of temporary captivity in hihi, whereby delaying release (even by 4 days instead of releasing immediately) decreased hihi survival (Richardson *et al.*, 2013). Overall, we stress the importance of collecting evidence on multiple costs and benefits of different release protocols, so that these can be weighed under clear reintroduction objectives to manage the translocation pathway effectively: for example, under some contexts disrupting social bonds post-release could be beneficial, such as if related individuals are translocated together and an aim is to prevent inbreeding.

Improving reintroductions requires adopting experimental methods to rigorously test potential intervention methods, however such study designs often face restrictions such as limited sample sizes and logistical constraints (Kemp *et al.*, 2015; Taylor *et al.*, 2017). Our study also suffered from these, as the number of birds moved was limited, we were restricted by existing aviary facilities, and we were unable to target capture of specific individuals. Nevertheless, by

experimentally testing for social changes during a reintroduction, we have provided important information to help target use of limited resources during conservation management of hihi and similar species. Overall, we highlight an as-yet little explored application for SNA to understand how social groups respond to conservation interventions, and suggest predicting sociality change should be a focus of future work.

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Author contributions

Author contributions (following CRediT taxonomy): Conceptualization, VF, JE, RT; Methodology, VF, JE, MM, KP, RT; Investigation, VF, CA, MM, KP; Data curation, VF, MM, KP; Analysis, VF, JE, RT; Writing (original draft and editing), VF, CA, JE, MM, KP, RT.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Frequency of different maximum re-sighting times for individual hihi from the observation data recorded in group sites.

Figure S2. Frequency of different event lengths generated using asnipe package to construct networks from (a) observation data and (b) PIT tag data collected in 2016.

Table S1. Ranking by quasi-likelihood Akaike information criterion of all models to explain variation in inter-survey survival (ϕ) depending on sex and time, with and without covariate (degree rank change) for (a) translocated and (b) non-translocated hihi. Models also account for variation in re-sighting likelihood (ρ).

Appendix S1. Deciding an appropriate length of time to define hihi group associations.